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Catch in the Primary Spines of the Sea Urchin *Eucidaris tribuloides:* A Brief Review and a New Interpretation

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Abstract. Previous models of reversible catch in echinoid spines, as a property of muscle or of collagen, are briefly reviewed and discussed. This brief review offers a new interpretation of catch in primary spines of *Eucidaris tribuloides*, viewing the collagen and small muscles of the catch ligament working together as a variable-length tendon. In the model presented, changes in ligament length when out of catch are accommodated by sliding of discontinuous, interdigitating and cross-link-stabilized columns of collagen fibrils, the muscle layer external to the ligament effecting spine movement. Catch is viewed as a consequence of contraction of small muscles inserted on the collagen columns within the ligament. Ligament shortening tightens the profuse (*ca.* 30,000/mm^2) and highly ordered collagen insertion loops within the stereoms of the spine base and test, and catch results from the multiplicative effect of these friction sites in series. New data are presented on novel structural cross-links between collagen fibrils. The cross-links stabilize the ligament columns. The central ligament in *Eucidaris* plays a purely passive mechanical role in maintaining the alignment of the spine-test articulation. It contains no muscle and neither contracts nor undergoes catch; its insertions are simple, unlike the complex stereom insertions of the main ligament.

Introduction

From the time that it was first recognized, the phenomenon of catch in sea urchin spines has attracted the interest of investigators, but its basis has remained unclear. Two seemingly contradictory theories have been proposed to explain catch; but recent experimental observations allow a new interpretation that reconciles the two discrepant hypotheses.

Catch is an operational concept that can be defined in this instance as a reversible, neurally controlled enhancement of the passive mechanical resistance offered by the spine test articulation (Fig. 1) to forces tending to change the position of the spine. The sudden inducement of catch freezes the primary spines in their respective positions, whether normal to the test surface or angled from this axis, thereby allowing the animal to maintain a fixed posture for long periods.

von Uexküll's catch muscle

At the turn of the last century, Count Jakob von Uexküll, a self-supporting German biologist noted for his strong vitalist convictions, published a paper (1900) titled "The Physiology of the Sea-urchin Spine" in which he reported that the voluntary and reflex movements of the spine are powered by a thin layer of muscle fibers that surrounds the thick articular capsule. In addition, he found that the integrity of this capsule, which is also known as the spine ligament or catch apparatus, is essential for the development of catch.

Von Uexküll described the breakage of the capsule by forcible displacement of the spine while in catch: spines treated in this manner failed to show catch, but they retained the ability to perform voluntary and reflex movements because the thin muscle layer was not disrupted. Accordingly, von Uexküll called this muscle layer *Bewegungsmuskulatur* (motion-supporting muscle) as opposed to the articular capsule, which he believed also to be a muscle, the *Sperrmuskulatur* (catch or holding muscle). As we shall see below, this was an inspired guess that

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Figure 1. The spine-test articulation of *Eucidaris*. In this Chlorox-digested preparation a small area of ligament remains, maintaining the ball-and-socket arrangement. × 18

defied contemporary evidence, because the latter tissue had been studied by 19th century microscopists (Prouho, 1887; Hamann, 1887) and was recognized by them as being primarily a connective tissue.

Takahashi's mutable connective tissue

The problem of catch in echinoderm spines was studied again in the 1960s by Takahashi (1966, 1967a, b, c), who confirmed von Uexküll's results while disagreeing with him on the nature of the ligament. In the discussion of his landmark paper (1967b) on "Responses to stimuli," Takahashi gave an account of the experimental results that led him to propose a new hypothesis to explain catch.

Because at that time the ligament was still regarded as a muscle, Takahashi first attempted to record its contraction following the application of chemical or electrical stimuli. He was not successful. Yet Takahashi was greatly impressed by the effects of the same chemical stimuli on the rate of elongation of ligaments subjected to a constant load (isotonic recording; creep test). In his words "the effects were clear, sometimes even dramatic, and they varied according to the kind of drug applied." Lengthening was retarded by acetylcholine, while adrenaline exerted an accelerating effect.

These observations led Takahashi to seek the identity of the structural element responsible for the ligament extension under constant load, and he saw a plausible candidate in the collagen. He accounted for his results on the premise that the mechanical consistency of collagen can switch reversibly between two extreme conditions or states: one pliant and extensible and the other stiff and inextensible. This hypothesis was attractive because it explained a variety of experimental observations and was accepted by most workers including ourselves (Morales *et al.*, 1989, 1993). This view gave rise, more or less directly, to the concepts of "connective tissue catch" (Rüegg, 1971), "mutable connective tissue" (Eylers, 1982) and "variable tensility" (Wilkie, 1984).

Takahashi's observations had a great impact on the study of echinoderm connective tissue, and it is now accepted that the members of each of the five extant classes of the phylum possess some connective tissue with properties that differ significantly from those of vertebrate collagen (Motokawa, 1984, 1985). In this context, we stress that the present account deals only with the primary spine ligament of *Eucidaris tribuloides*, and while we do not extrapolate our conclusions to other echinoderms, neither do we suggest that our model of catch is restricted to this echinoid.

The Ligament as a Myotendinous Organ

Muscle fibers

The fine structure of the ligament was first studied by Smith *et al.* (1981) and Hidaka and Takahashi (1983), who noted the presence of muscle fibers in the spaces between the cylinders or columns of collagen fibrils that occupy most of the volume. As described by the above authors, the muscle cells are slender (only about 0.1–1 μm in diameter) and unstriated, and they include large paramyosin filaments in their contractile array. They make only a small contribution to the volume of the ligament: about 1.5% of the cross-sectional area in our micrographs of *Eucidaris*. We have determined that they insert directly onto the collagen columns. Although we lack information about their length and arrangement, the almost exact alignment of the muscle fibers and the collagen columns in transverse sections suggests that the two are virtually parallel, and we view the muscle as probably extending between adjacent collagen columns.

In addition, Hidaka and Takahashi suggested that changes in length of the ligament might reflect sliding within the array of collagen fibrils, and that catch could be accounted for by the formation of cross-links between the sliding elements. This suggestion stimulated work and speculation on the nature of the proposed cross-links, which were pictured variously as simple divalent cations, notably calcium (Hidaka, 1983; Diab and Gilly, 1984), and proteoglycans binding together the collagen fibrils (Trotter and Koob, 1989).

Insertion of the muscle fibers

Working on *Anthocidaris*, Hidaka and Takahashi (1983) noted that the muscle fiber surfaces were very closely apposed to the peripheral fibrils of the collagen columns and, while favoring the view that the muscles are long, running from insertions on collagen near the

spine base and test, they suggested that the muscle cells might be relatively short and serve as cross-links between the collagen columns. They further described the fine structure of the ligament stretched to three times its resting length, noting "empty spaces" in the collagen array. They attributed this pattern to the slippage of collagen fibrils relative to one another. Thus they regard the individual collagen fibrils as the units responsible for sliding during forced ligament elongation. In contrast, we view the columns, rather than individual fibrils, as the functional units of the ligament length change accomplished by sliding. Each column is separated from its neighbors by 'matrix spaces,' but there is no fine structural evidence of cross-links between columns; *i.e.*, between the peripheral fibrils of adjacent columns. We suggest that the linkage between columns is effected by the muscle fibers.

We offer a rather different interpretation of Hidaka and Takahashi's micrographs: namely, that during irreversible, non-physiological stretching, peripheral portions of discontinuous collagen columns are torn away at the region where the muscle fibers are firmly inserted onto the columns. Before describing our reinterpretation of Hidaka and Takahashi's experimental findings, however, we should introduce a further piece of evidence concerning the collagen columns in *Eucidaris*.

Structure of the collagen columns

Other than the presence of transient links invoked in previous models of catch, the columns have been regarded as groups of mechanically independent fibrils. Indeed Hidaka and Takahashi's model is based on this assumption. But, in *Eucidaris* (Figs. 2, 3) we have observed a novel feature in conventionally prepared material[1], the fibrils of each column are profusely cross-linked by asymmetrical junctions and by apparently different, simpler, and symmetrical bridges; a single large-diameter fibril profile often shows multiple links with its neighbors. The apparent stability of the collagen columns seen in the transverse plane is also suggested by the regularity of organization of the columns seen in longitudinal sections (Fig. 6). Not only are individual fibrils precisely parallel, but some degree of register is often seen in the striation pattern of adjacent fibrils. As previously noted by Scott (1988) in the holothurian body wall and in vertebrate tendons, and by Trotter and Koob (1989) in *Eucidaris*, proteoglycan strands form a regular meshwork between the fibrils. In *Eucidaris* the regularity of their placing with respect to the fibril striations is noteworthy (Fig. 6), although their function remains undetermined. Proteoglycans are visualized only after special tissue preparation (Scott, 1980, 1988), and it is unlikely that the cross-bridges seen in conventionally prepared material, mentioned above, are related to the proteoglycan moieties of the columns. Although the nature of these bridges remains unknown—and neither type matches the fine proteoglycan strands described by Scott in tendon, by Trotter and Koob in *Eucidaris* ligament, and shown here in Figure 6—we regard this elaborate system as likely to give added mechanical stability to each column as a structural unit.

Trotter and Koob's model

Trotter and Koob (1989) reported a model of the ligament in which the collagen fibrils are the discontinuous fiber phase of a fiber-reinforced composite material. Their measurements of single isolated collagen fibrils revealed that, although varying in length and radius by more than an order of magnitude, they have a high and constant length/radius ratio, which was interpreted as indicating that the non-fibrillar material must act to transfer stress between fibrils. Trotter and Koob suggested that proteoglycan "may be an important component of the stress-transfer matrix," and illustrated the regular disposition of this material with respect to the collagen band pattern. We repeated this, with similar results (Fig. 6). But such proteoglycan components seem to be commonly associated with collagen, including that of vertebrate tendon (Scott 1980, 1988).

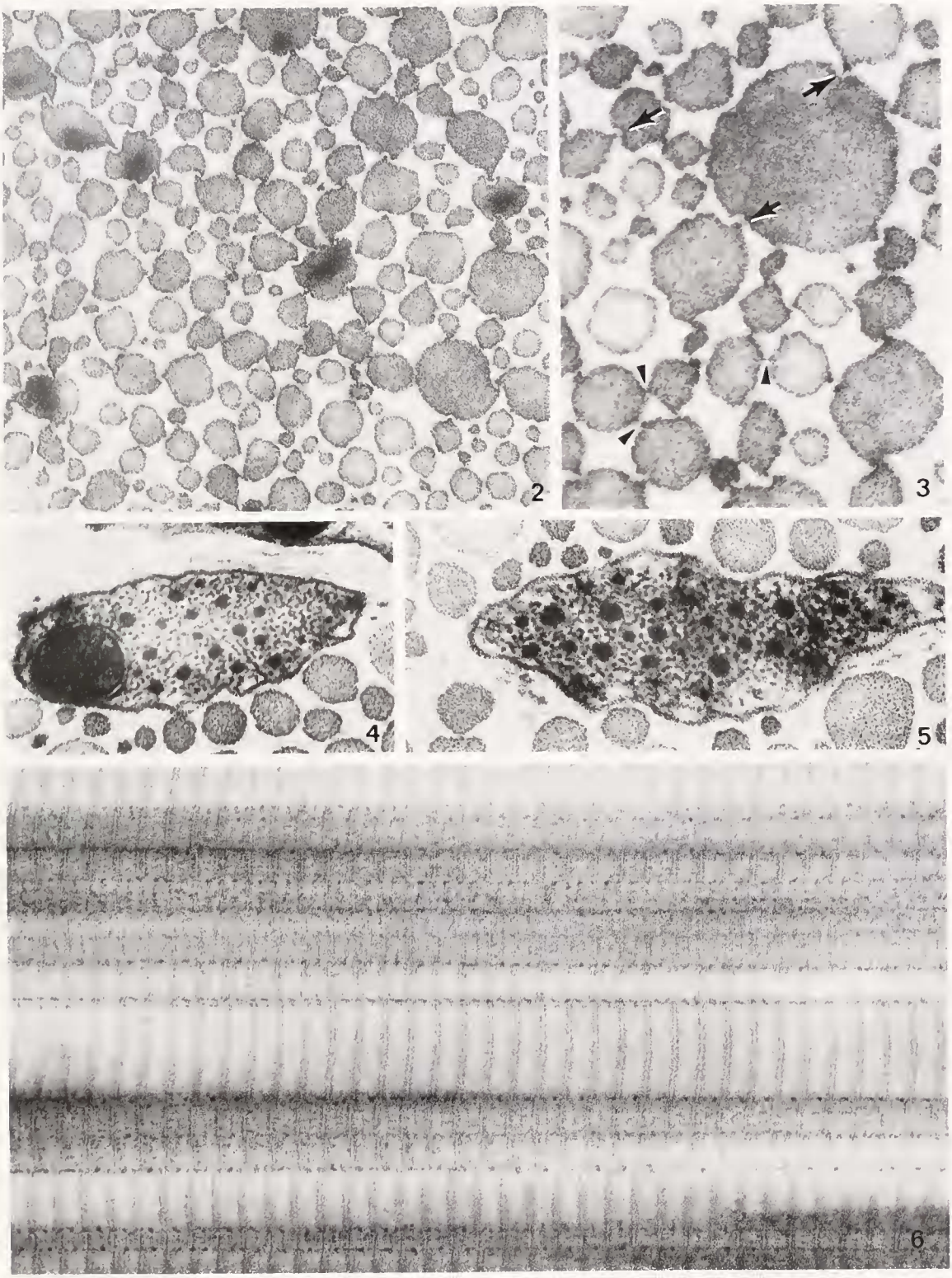
Nature of the sliding elements in the collagen array

We envisage ligament length change as being accomplished by a sliding movement between stabilized, discontinuous, and interdigitating columns. Adopting this view, we see Hidaka and Takahashi's observations in a different light. First, we noted, in *Eucidaris*, a very close apposition of muscle cell surface to column periphery, as Hidaka and Takahashi reported in *Anthocidaris*: *i.e.*, a gap of only about 10 nm separates the muscle plasma membrane from the outermost collagen fibrils, and this membrane is often contoured to match the fibrillar surfaces (Figs. 4, 5). Whereas Hidaka and Takahashi favored the view that the muscle fibers run from insertions near the spine base and the test, the high frequency with which

[1] Material illustrated in Figures 2–5 and 10 was conventionally fixed (2.5% glutaraldehyde, 0.05 *M* cacodylate buffer pH 7.4 with 14% sucrose), treated with 1% OsO_4 and embedded in Araldite. Contrast was enhanced on the grid by treatment with lead citrate followed by unbuffered 1% $KMnO_4$. Proteoglycans (Fig. 6) were visualized by the method of Scott (1980, 1988); low contrast enhancement of the collagen was obtained by treating sections with lead citrate alone. Material for SEM examination was fixed as for thin sectioning, but without OsO_4 treatment, and critical point dried. Details of preparation of frozen-fractured material (Fig. 9) are given in Smith *et al.* (1990).

Figure 2. Transverse section of collagen fibrils. Note the frequent inter-fibrillar cross-links, shown further in the next figure. ×60,000

Figure 3. The collagen filaments of the ligament are linked by frequent asymmetrical (arrows) and symmetrical (arrowheads) cross-bridges. ×110,000



Figures 4, 5. Illustration of the close apposition of muscle fibers and collagen fibrils in the main ligament of *Eucidaris*. A gap of about 10 nm separates the fiber plasma membrane from the collagen surface, and the membrane is often indented around the fibrilar contours. Figure 4, ×90,000; Figure 5, ×120,000

Figure 6. Longitudinal section of the main ligament in *Eucidaris*. Proteoglycan is visualized by staining with cuprolinic blue. Note the precisely parallel disposition of the fibrils and areas of alignment of collagen banding. ×72,000

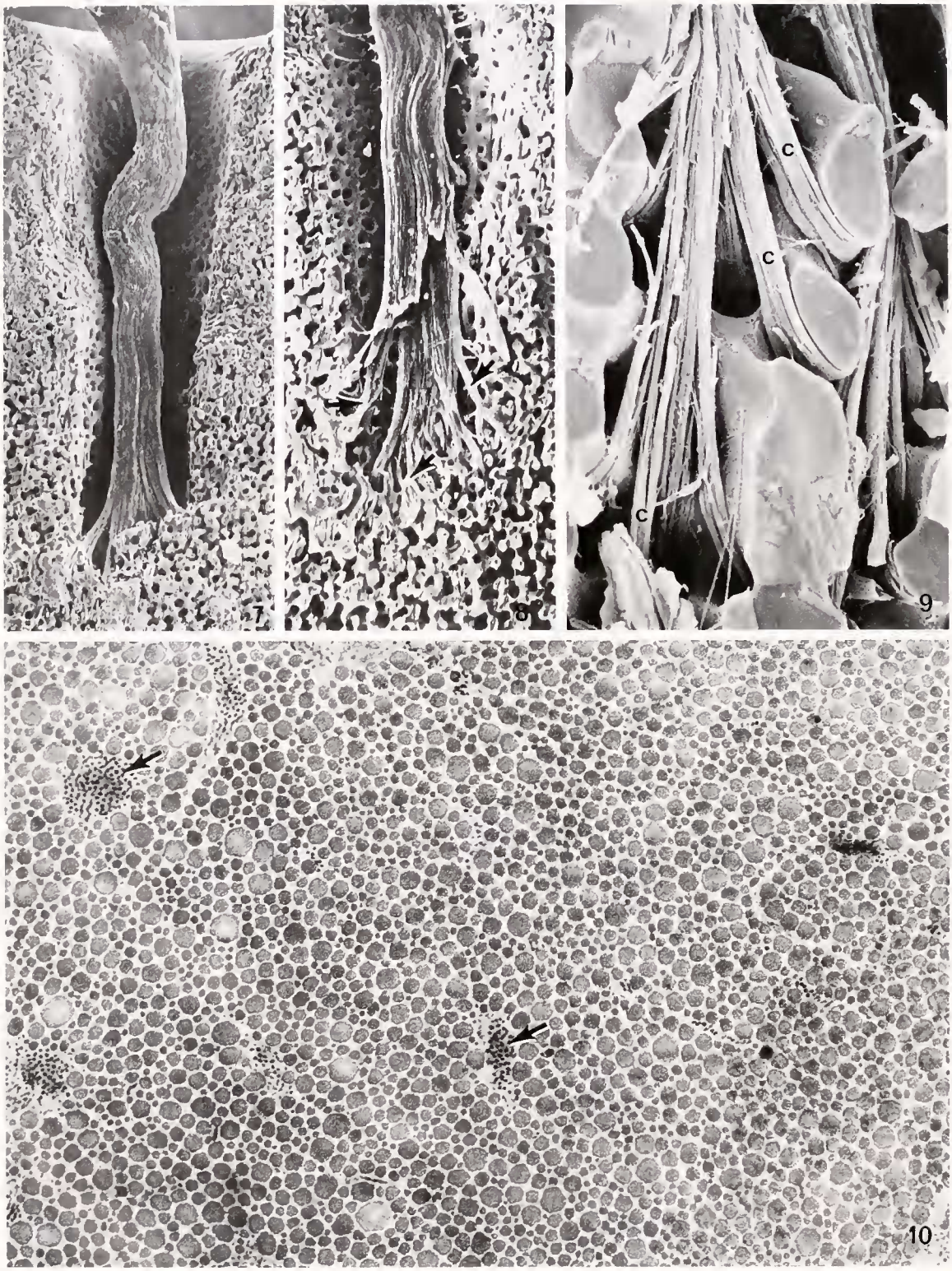


Figure 7. SEM of the insertion cavity and the central ligament on the test of *Eucidaris*. ×90

Figure 8. As in Figure 7, but with insertion of the central ligament exposed. The ligament ramifies into slender processes (arrows), which loop through stereom trabeculae. ×130

Figure 9. SEM of frozen-fractured main ligament insertion on the *Eucidaris* test. Note collagen straps (c) looping through stereom trabeculae and tightly appressed to the stereom struts. (From Smith *et al.*, 1990). ×1,500

we have observed muscle insertions on thin sections of the ligament led us to the alternative view that the muscle fibers are very numerous and relatively short, linking adjacent collagen columns throughout the ligament. A reexamination of their figures (*i.e.*, Hidaka and Takahashi, 1983, Figs. 8, 9) suggests that stretching somewhat distorts but does not obscure the arrangement of collagen columns and that the 'holes' appearing in the transversely sectioned array are not random but represent lenticular gaps where bundles of fibrils have been torn apart. In addition we regard the muscle fibers as very strong, as shown, for example, by the presence of highly stretched but essentially intact muscle fibers in pictures published by Hidaka and Takahashi (1983). The linkage between muscle fibers and columns must be strong if our model is correct.

Although there is no fine structural evidence of discontinuity, it seems likely that the columns taper at their ends. Profiles of 'tiny' columns are dispersed in transverse sections, probably columns near their ends (see Fig. 3).

The Ligament Contracts

In view of the presence of contractile cells, one should expect that cholinergic agonists would induce some mechanical effect on the ligament. The very modest contribution of muscle to the volume of the ligament seemed to rule out a leading role for them in ligament mechanics analogous to that of muscle in the molluscan catch mechanism. Indeed, the only functional alternative that Smith *et al.* (1981) suggested was the relatively minor task of returning an extended sector of the ligament to its 'normal' position.

To obtain further information on the physiological properties of the ligament, we reinvestigated its responses to electrical and chemical stimuli. We found that the ligament behaves as an excitable motile tissue, shortening and developing a mechanical force following the application of either type of stimulus (Vidal *et al.*, 1983). The most probable explanation of the discrepancy, in identical experiments, between our positive results and the negative ones of Takahashi is that prior to stimulating the ligament, we treated it briefly with tyramine (1 m*M*, 2–5 min). This compound, like its close analog octopamine, exerts a lytic effect on catch and a relaxing effect on contraction (Morales *et al.*, 1989). The use of tyramine allowed us to work with a fully relaxed preparation in every experiment. In addition, we applied a force of 2 to 3 g, which tends to separate the two calcareous moieties of the spine-test joint. By comparing the kinetics of the catch with the contracture induced by cholinergic agonists on the same preparation, we concluded that these phenomena are two sides of the same coin. In other words, we believe that catch is simply the expression of the shortening of the ligament.

Mechanism of Catch

We must now consider how the contraction of the ligament opposes, or counteracts altogether, the passive movements of the spine. An answer to this question must explain how the force generated by the scant and slender muscle fibers can overpower the stresses generated, often with considerable mechanical advantage, by the external forces acting on the shaft of the spine. The fine structure of the essentially simple but highly ordered insertions of the ligament onto the stereom in *Eucidaris* was described by Smith *et al.* (1990) and revealed an order first hinted at in the light micrographs of Takahashi (1966). Within the stereom, the collagen columns divide into a series of successive, parallel slender straps, passing reflexively across struts or microbeams that border spaces considerably wider than the straps they accommodate. In most micrographs obtained by Smith and co-workers, the straps appear to be tightly cinched to the struts (see Fig. 9), but they are sometimes seen lying free within the lacunae, suggesting that they are not 'glued' immovably to the stereom microbeams. The lacunae are sufficiently wide to permit some movement of the straps when disengaged.

An answer to the main question posed above may be found in the frictional resistance generated at the ligament insertions by minute but crucial movement of the straps over the struts. As the friction between two sliding surfaces is proportional to the force that keeps them together, the resistance between straps and struts will be modulated by the muscle fibers in parallel with the collagen columns. In this model, shortening of the ligament that initiates catch will increase the force that presses the straps upon the struts, thereby increasing the friction between these two structures.

Our model of catch is shown in Figure 11. In the absence of cholinergic stimulation, the muscle fibers will be relaxed and, therefore, the ligament will be slack. The straps will rest loosely on the struts, and the spine-test joint can be moved passively without offering significant resistance. As muscle contraction starts to tighten the ligament, a very small change in the position of the straps is envisaged as introducing frictional resistance at the sites where they appressed the struts within the stereom. The friction between the surfaces of both structures, according to this model, will absorb the energy applied by external forces. The model further emphasizes that, rather than

Figure 10. Transverse section of *Eucidaris* central ligament. Note that the collagen forms a continuous array largely filling the field. Groups of microfilaments are present (arrows) but nerve processes and muscle cells are absent. ×30,000

acting as a work-generating device, the function of the muscle fibers of the ligament seems to be (like the braking pedal of a car) that of controlling an energy-absorbing or energy-dissipating system, similar in design to an automotive friction brake, engineered to take advantage of the roughly 30,000 bands or straps underlying each square millimeter of the insertion surfaces both at the spine base and test. The resistance generated at single strap-strut contacts will be greatly amplified by the multiplicative effect of friction sites in series.

The Central Ligament

A final piece of evidence in support of the above model is provided by comparing the structure and function of the main ligament and a supplementary structure, the central ligament, that is present in many echinoid spines including those of *Eucidaris*. The central ligament extends across the midpoint of, and inserts into cylindrical cavities in, each surface of the spine-test articulation (Cuénot, 1948; Hyman, 1955). Motokawa (1983) described this structure in *Diadema setosum*: it is relatively robust, about 0.5 mm in diameter, and responsible for maintaining the attachment between spine and test, even when the joint is dislocated by extreme spine declination (Takahashi, 1967c). In our observations on *Eucidaris* (Fig. 7), the corresponding structure is <0.1 mm in diameter, considerably smaller in relation to the articulation than in *Diadema*. The central ligament in *Eucidaris* differs strikingly in both fine structure and stereom insertion from the main ligament. First, the collagen fibrils form a continuous and compact block that is not divided into discrete columns (Fig. 10). Second, it contains neither muscle cells nor granule-containing neurites. In common with the main ligament, collagen straps do enter the stereom, but they loop irregularly through cavities of the unmodified, tetragonal, stereom fabric (Fig. 8), and the elaborate system of struts and straps of the main ligament is absent. Furthermore, we were unable to detect any mechanical response to acetylcholine in the central ligament in contrast to the contracture and catch elicited in the main ligament. We view the central ligament in *Eucidaris* as a physiologically inactive link, presumably safeguarding the alignment of the articulation during spine movement.

The structural peculiarities of the central ligament are consistent with our view of the way in which the main ligament achieves the catch state. Without muscle fibers, the central ligament cannot shorten. Because the central ligament does not undergo length change and is not involved in catch, the collagen is arranged for maximal tensile strength, not to accommodate an intra-ligament sliding movement. Rather than being arranged in interdigitating columns, as in the main ligament, the collagen fibrils are disposed as a continuous block virtually filling the structure. In the main ligament, columns of collagen fibrils

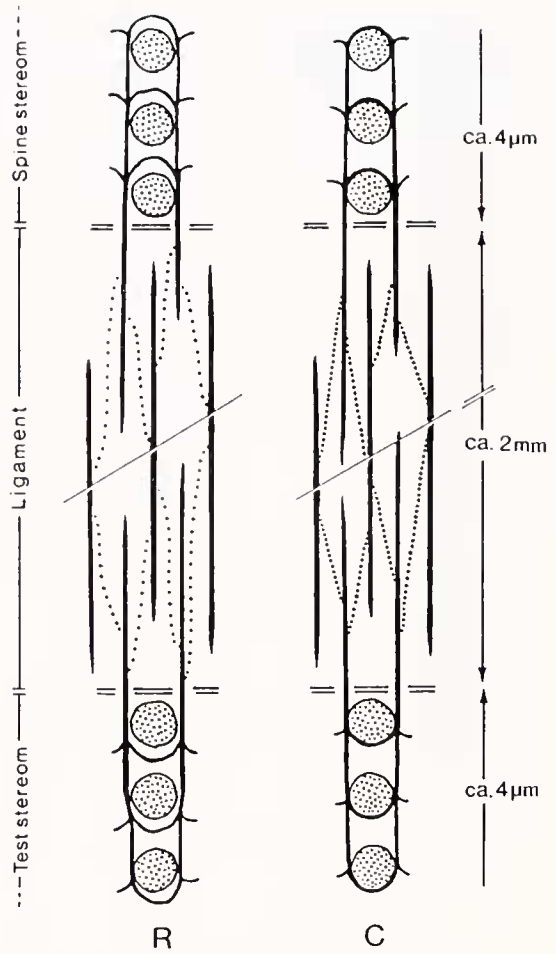


Figure 11. Schematic diagram of model discussed in the text. *R* relaxed ligament; *C* contracted ligament. Approximate dimensions of the spine and test stereom, and the ligament, included in the diagram are indicated; note the great difference in scale. *Stippled circles* represent transverse profiles of stereom struts: only three struts are shown in each stereom (of the five or six actually present in each row). In *R* the collagen straps are represented as looping loosely between the struts; in *C* they are tightly applied to the struts. In *R* relaxed muscle fibers inserting on collagen cylinders of the main ligament are represented by wide-spaced dotted lines (. . . .); in *C* contracted fibers are represented by close-spaced dotted lines (. . . . .).

are stabilized by cross-links; we suggest that similar links present in the central ligament stabilize it for its purely passive, mechanical role. Furthermore, the central ligament, stressed only by spine movement, is well-served by an unspecialized anchorage, contrasting with the precise arrays of collagen straps and stereom struts of the main ligament, discussed above.

Our findings in *Eucidaris* differ in important respects from those of Motokawa (1983) in *Diadema*. He found the central ligament physiologically similar to the main ligament, its viscosity was increased by acetylcholine and decreased by epinephrine. He suggested that the central ligament is mechanically and structurally similar to the

main ligament, except for the apparent absence of muscle fibers in the former. Moreover, in *Diadema* the collagen fibrils are grouped in columns in both main and central ligaments. Other than noting the very different functions of spines in *Eucidaris* and *Diadema*, we can at present only draw attention to these discrepancies, not account for them.

Conclusions

In the model of catch we have proposed, we view evolutionary experimentation as providing a solution to the problem of minimizing muscle tissue mass, while achieving maximal efficiency. Indeed, a catch apparatus that would meet the mechanical needs of the spine, but made up of conventionally arranged muscle fibers, might be too 'expensive' for the very limited energetic resources of the sea urchin (Bianconcini *et al.*, 1985). The layer of conventional muscles external to the ligament is responsible for moving the spine, whereas the muscle of the catch system was diverted from power generation to the regulation of the energy-absorbing function of the ligament. In a sense, von Uexküll and Takahashi were both correct in seeing catch as a property, respectively, of muscle and collagen. The spine ligament, with its catch capacity, may be regarded as a myotendinous organ that combines in a uniquely efficient manner the contractile properties of muscle with the tensile strength of collagen fibrils, to produce a variable-length tendon.

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